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**The Cophylogeny of Populations and Cultures:
Reconstructing the Evolution of Iranian Tribal Craft
Traditions Using Trees and Jungles**

Jamshid J. Tehrani ^{1,2,†}, Mark Collard ^{2,3} and Stephen J. Shennan ^{2,4}

¹Evolutionary Anthropology Research Group, Department of Anthropology, Durham University, Durham, UK.

²AHRC Centre for the Evolution of Cultural Diversity, University College London, London, UK.

³Laboratory of Human Evolutionary Studies, Department of Archaeology, Simon Fraser University, Burnaby, Canada.

⁴Institute of Archaeology, University College London, London, UK.

[†]To whom correspondence should be addressed: Jamshid J. Tehrani, Department of Anthropology, Science Site, South Road, Durham University, Durham DH1 3LE, UK. Tel: 44 (0)191 334610. E-mail: jamie.tehrani@durham.ac.uk.

Abstract

Phylogenetic approaches to culture have shed new light on the role played by population dispersals in the spread and diversification of cultural traditions. However, the fact that cultural inheritance is based on separate mechanisms from genetic inheritance means that socially transmitted traditions have the potential to diverge from population histories. Here, we suggest that associations between these two systems can be reconstructed using techniques developed to study cospeciation between hosts and parasites and related problems in biology. Relationships among the latter are patterned by four main processes: co-divergence, intra-host speciation (duplication), intra-host extinction (sorting) and horizontal transfers. We show that patterns of cultural inheritance are structured by analogous processes, and then demonstrate the applicability of the host-parasite model to culture using empirical data on Iranian tribal populations.

Key words: cultural phylogenies; population history; coevolution; cophylogeny; cultural evolution; Iranian tribes

Introduction

The extent to which cultural traditions track the descent histories of populations has long been debated. For most of the last century, the consensus among anthropologists and archaeologists has been that any evidence relating to the historical origins of cultural assemblages would probably be swamped by the rapid rate of cultural evolution, and by the effects of trade, intermarriage and exchange among neighbouring groups (e.g. Boas 1949, Kroeber 1948, Moore 1994). However, recent applications of techniques of phylogenetic analysis borrowed from biology have succeeded in reconstructing coherent and long-lasting lineages of cultural inheritance across a number of domains (e.g. Mace et al., 2005, Lipo et al., 2006). For instance, analyses of relationships among languages suggest that resemblances among word forms can often be traced back to ancestral speech communities that existed many thousands of years ago (e.g. Gray and Jordan 2000, Gray and Atkinson 2003, Kitchen et al. 2009). Similarly, it would appear that many craft styles and technologies are

handed down from generation to generation, eventually giving rise to new forms that are recognisably derived from their parent tradition (e.g. Buchanan & Collard 2007, 2008, Collard & Shennan 2000, Lycett 2007, 2009, O'Brien & Lyman 2003, Tehrani & Collard 2002, 2009a, 2009b).

The reconstruction of such lineages can provide useful evidence about the origins and dispersal of populations, especially in cases where genetic data are scarce or noisy. For example, phylogenies derived from cultural traits have been used to test competing hypotheses about the colonisation of the Pacific (Gray & Jordan 2000, Gray et al. 2009, Rogers et al. 2009), the Bantu expansions in Africa (Holden 2002), the origins of the Indo-Europeans (Gray & Atkinson 2003) and the peopling of the Americas (Buchanan & Collard 2007). However, while most studies indicate that cultural phylogenies and population histories are usually highly correlated (e.g. Gray & Jordan 2000, Holden 2002, Tehrani & Collard 2002, 2009a, 2009b), the match is not always perfect. For example, Tehrani and Collard noted that some of the relationships among Turkmen (Tehrani & Collard 2002) and rural Iranian (Tehrani & Collard 2009a, 2009b) weaving traditions contradict written and oral histories about the tribes' origins. Similar inconsistencies have been reported in reconstructions of indigenous Californian basketry assemblages (Jordan & Shennan 2003), Siberian material culture (Jordan & Mace 2006), Baltic stringed instruments (Temkin & Eldredge 2007) and Polynesian canoes (Rogers et al. 2009).

To shed more light on these issues, we draw on ideas from dual inheritance theory or gene-culture coevolutionary theory (e.g. Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981, Durham 1990, Richerson & Boyd 2005). Dual inheritance theory views culture and genes as separate but coevolving systems of heritable variation, each based on autonomous mechanisms of information transmission (i.e. imitation and teaching versus biological reproduction). At the individual level, this requires models that can account for the interactions between genetic traits, which can only be transmitted "vertically" from parents to offspring, and learned behaviours that can be acquired vertically, "obliquely" from other adults, or "horizontally" among members of the same generation (ibid.). Similar models are needed at the group level. These would recognise that, while cultural traditions and populations may be closely linked, the processes involved in their propagation, dispersal and extinction are ultimately

independent of one another. The main aim would then be to understand what kinds of processes lead to correlations between cultural phylogenies and population histories, and what kinds of processes lead to divergences. Following the suggestions of Jordan and Mace (2006), Gray et al. (2008) and Riede (2009), we argue that such a model can be developed from the study of long-term co-evolutionary, or “cophylogenetic”, relationships in biology.

The cophylogenetic framework

The study of cophylogeny spans several domains in biology, including cospeciation in host and parasite organisms, the reconciliation of species trees and gene trees, and associations between species histories and area histories in vicariance biogeography (e.g. Brooks & McLennan 1991, Page 2003). The key issue in each of these endeavours is essentially identical to the one we face here. It concerns how far the history of one group of entities (i.e. the parasites, genes, organisms, or cultural traditions) is determined by the history of another group (i.e. the hosts, species, geographical areas or populations). This is addressed by mapping a dependent phylogeny (i.e. the parasite, gene, or organism tree) onto an independent phylogeny (the host, species, or geographical tree). Historical relationships between the two systems of interest can then be described in relation to four generic processes: co-divergence, sorting, duplication and horizontal transfer (e.g. Page 2003) (Figure 1). Each of these processes can be readily identified in cultural evolution.

FIGURE 1 ABOUT HERE

1. Co-divergence

In co-divergence, the dependent lineage splits as a result of the independent lineage splitting. In the case of hosts and parasites, co-divergence is equivalent to cospeciation, and typically occurs when the speciation of a host organism results in the speciation of associated parasites (e.g. Hafner & Nadler 1988). In molecular phylogenetics, co-divergence occurs when a genetic lineage diverges into daughter lineages coincident with a speciation event (interspecific coalescence), while in biogeography a co-divergence takes place when a new species arises in geographic isolation as a result of a geological event (vicariance) (e.g. Hafner & Page 1995,

Ronquist 1998). In all these instances, co-divergence results in a direct correspondence between the dependent and independent phylogenies.

In the case of cultural evolution, co-divergence is equivalent to the division of cultural traditions resulting from population splits, which is often associated with the demographic expansion of populations. The impact of co-divergence in generating cultural patterns is exemplified by the spread of agriculture. The Neolithic expansions in Europe, Oceania and Africa not only left strong genetic signatures, but also were associated with the growth and spread of distinct language families (e.g. Gray & Atkinson 2003, Gray & Jordan 2000, Holden 2002). In each of these cases, new languages appear to have evolved primarily as a result of population dispersals.

2. Sorting

In host-parasite studies, sorting refers to the extinction of a parasite lineage within a host lineage. Sorting events can also occur as a result of a parasite ‘missing the boat’ when a descendent of the host species does not inherit all the latter’s parasites (e.g. Paterson et al. 1999). The extinction of a genetic lineage within a species or of a species in a habitat is also classified as a sorting event (e.g. Hafner & Page 1995, Page & Charleston 1998). Sorting can be thought of as the pruning of some branches on the dependent phylogeny, which results in mismatches with the tips of the independent phylogeny.

Sorting events are likely to be common in cultural and linguistic evolution. Globalised capitalism and the spread of modern communications systems has caused (or at least coincided) with the decline of innumerable dialects, technologies and other cultural practices associated with indigenous peoples around the world. For example, Ohmagari and Berkes (1997) found that traditional bush skills are in decline among the Cree of James Bay, Canada, because their communities no longer depend on hunting and fishing for subsistence. Instances of cultural loss are also known from historical evidence. One of the most dramatic of these occurred in Tasmania. Archaeological evidence suggests that the first humans to arrive in Australia possessed a relatively sophisticated set of weapons, tools and crafts. While many of these were maintained by mainland groups, in the 10,000 years prior to the arrival of the first Europeans, native Tasmanians appear to have lost techniques required to fish,

prepare furs, make bone tools, arrows and boomerangs and even the knowledge required to make fire (Henrich 2004).

3. Duplication

In duplication, the branches of the dependent phylogeny split but the branches of the independent phylogeny do not. In other words, duplication events create mismatches between the dependent phylogeny and independent phylogeny by adding branches to the dependent phylogeny. In the host-parasite case, this equates to the intra-host speciation of a parasite species. In genetics, duplication results in an organism carrying two copies of the same gene. In the case of organism-area associations, duplication is equivalent to sympatric speciation, which occurs within an undivided geographical area or habitat range (Page & Charleston 1998).

The history of sport is replete with examples of cultural duplication. For instance, modern football and rugby are descended from ball games played in nineteenth century England that were not recognisably distinct from one another. It was only after the establishment of separate governing bodies who formally codified the rules that the two sports diverged. A later schism gave rise to separate codes of Rugby League and Rugby Union. Like the earlier split from football, the diversification of these sports occurred within an undivided population and can therefore be classed as a duplication. Duplication can also be seen in the diversification of religious sects and denominations. Although ideological disputes can result in congregations dividing into separate communities of worship, this does not usually result in the formation of genetically, ethnically or linguistically distinct populations. In modern societies, members of different religious communities frequently intermarry and may even change their faith several times over their lives. These examples show how cultural lineages can diversify independently of the populations which they are associated with.

4. Horizontal transfer

Some parasite species colonise new hosts via a process known as 'switching'. Switches are described as horizontal transfers because they involve a host acquiring a parasite from a non-ancestral species that they have come into contact with. This process can lead to major discrepancies between the phylogenies of the two groups of

species (Page 2003). Horizontal transfers can be similarly problematic in other areas. In molecular evolution, horizontal transfers, or ‘reticulations’, are considered rare but are known to occur in some organisms, such as the exchange of plasmid DNA in bacteria. This can greatly complicate the reconstruction of these organisms’ phylogenies (Doolittle 1999). In biogeography, horizontal transfers are equivalent to the dispersal of a species from one region to another. In this context, the phylogeny of a group of species may not map well onto the geological histories of the territories in which they are found (e.g. Ronquist 1998).

Horizontal transfers are likely to be a significant problem in reconciling cultural traditions with population histories. There is considerable evidence that horizontal transfers can occur across a variety of domains. One such domain is technology, where useful innovations can spread far from their original point of origin through trade and contact among populations. This phenomenon has been extensively studied by anthropologists and archaeologists since the nineteenth century. For example, Balfour (1889) carried out detailed analyses of composite bows from the Pitt Rivers collection, literally dissecting them to examine their shared “anatomical” characteristics. Balfour (1889) proposed a Central Asian origin for the bow, which was then adopted and successively modified by populations who adopted it as it spread north to the Arctic regions and then west into Siberia and across the Bering Strait into America, west to Persia and Europe, and south to the Indian subcontinent. Similar kinds of processes have been documented in the spread of doctrinal religions as populations get converted by other populations they come into contact with. Buddhism is an excellent example. Buddhism emerged in India in the 6th century BCE. Within 200 years it underwent a massive expansion, spreading south to Sri Lanka, east into Indochina and northwest into Central Asia, eventually reaching China via the Silk Route (Conze 1980). While the central tenets of Buddhism remained more-or-less the same, specific doctrines and rituals were adapted by the various populations who adopted it. This gave rise to new traditions of Buddhism that are phylogenetically derived from India, even though many of their respective adherents are not.

Case study: the spread of weaving in Iranian tribal groups

The generic nature of the processes described above means that there has been considerable cross-over in the methods used to study cophylogeny in different biological contexts. We are not the first researchers to realise the potential value of extending them to cultural evolution. For example, Gray et al. (2008) have suggested that techniques used to reconcile gene trees with species trees could be useful for studying the ways in which word histories are embedded in language histories. Jordan and Mace (2006) and Riede (2009) have used methods to test for cospeciation in host and parasite lineages to explore historical correlations among different components of material culture assemblages (e.g. Jordan and Mace 2006, Riede 2009). In this section, we present a case study that applies a comprehensive co-phylogenetic framework to reconstruct historical relationships between cultural traditions and populations. The study focused on weaving traditions in seven Iranian tribal populations, whose geographical distributions are shown on the map in Figure 2.

FIGURE 2 ABOUT HERE

Unfortunately, there are currently no genetic data on the population histories of the tribes. However, it is possible to draw inferences about their origins and relationships to one another from linguistic affiliations and oral history (e.g. Amanolahi 1988, Barthold 1962, Grimes 2002, Oberling, 1974, Windfuhr 2007). These suggest that the populations can be divided into two main lineages. The first lineage comprises Iranian-speaking groups that are believed to have originated in western Iran (Amanolahi 1988). The groups are the Baluch, the Boyer Ahmad, and Bakhtiari. Members of this lineage can be further divided into the Baluch on the one side, and the Boyer Ahmad and the Bakhtiari on the other. The latter two groups speak Lori and inhabit the Zagros Mountains of western Iran. The ancestors of the Baluch are believed to have migrated from western Iran to the desert regions of southeastern Iran, western Afghanistan and northwest Pakistan some 900 years ago (Frye 1960, Thompson 2002), splitting from the ancestral population that gave rise to the Lurs (Amanolahi, 1988). The second main lineage comprises the Qashqai, Shahsevan, Tekke and Yomut. These populations claim descent from Oguz Turkic hordes that invaded Iran between the 10th and 12th centuries (e.g. Barthold, 1962, Beck 1986,

Oberling, 1974). All four of these groups speak Turkic languages. They can be subdivided into two sub-groups, one that speaks Turkmani, which belongs to the eastern branch of Oguz Turkic languages, and the other Azeri, which belongs to the western branch (Grimes 2002). The Yomut and the Tekke speak Turkmani. Both groups inhabit the northeastern region of Iran and Turkmenistan. The Shahsevan and the Qashqai speak Azeri. The Shahsevan are located in northwestern Iran close to the Caspian Sea. The ancestors of the Qashqai are believed to have also originated near the Caspian Sea, but migrated south to the Zagros Mountains about 500 years ago (Oberling 1974) where they are now neighbours of two of the Iranian-speaking groups, the Bakhtiari and Boyer Ahmad. The hypothesized migration histories of the tribes are shown on the map in Figure 2.

There are several reasons to suspect that the history of weaving traditions is likely to be strongly correlated with population histories. The first is that textile weaving is intimately connected to the nomadic-pastoralist mode of subsistence pursued by members of these communities until recently. Unlike objects made from other materials such as wood and metal, woven rugs, bags and bands can be folded or rolled and are therefore much easier to carry on long and physically challenging migrations between seasonal camps, which in some cases covered distances of hundreds of miles across difficult, mountainous terrain. Furthermore, the raw materials and equipment for weaving were easy to obtain locally: Wool can be sheared from sheep and goats, while in the past dyes were extracted from plants, insects and fruits. The second reason is that weaving skills are transmitted in a highly vertical and conservative fashion from mothers to their daughters (Tehrani & Collard 2009a). Endogamous marriage norms mean that females do not usually marry males from other tribes. This in turn implies that daughters do not generally inherit from their mothers craft traits that are foreign in origin. Lastly, even when weavers do adopt traits from non-maternal sources, they usually copy members of their immediate community. Social norms prevent women from travelling far from their father or husband's household, with the result that they have few opportunities to interact with weavers from other tribes (*ibid.*).

To reconstruct the history of the tribes' weaving traditions we carried out a cladistic analysis of 150 characters in each of the seven tribes' assemblages. The weavings of

the Qashqai, Bakhtiari and Boyer Ahmad were sampled by JJT during two field surveys carried out in southwestern Iran in May 2001 and September to December 2002. Data on the weavings of the Baluch, Shahsevan, Yomut and Tekke were gathered from published catalogues (Baluch: Konieczny 1979; Shahsevan: Tanavoli 1985; Yomut and Tekke: Thompson 1980, Tzavera 1984). The characters consisted of textile traits, including techniques of preparation and fabrication (e.g. spinning, knotting, etc.), the use of different materials (e.g. wool, goat hair, dyes, etc.) and variation in decorative features (e.g. carpet designs, border patterns, etc.). We used a prehistoric archaeological textile assemblage as an outgroup for the analysis. The assemblage comprised rugs, mats, and decorative felts excavated from the ice-filled tombs of a nomadic people that inhabited the Pazyryk valley in the Altai Mountains of Siberia in the 4-5th century BCE (Rudenko 1970). These artifacts provide the best available information on the roots of weaving among Central and Western Asian nomadic pastoralists and, as such, are a useful means of inferring the likely ancestral states of the characters used in the present study. The data matrix is provided in the Supplementary Materials.

The analysis was carried out in the software program PAUP 4.0* (Swofford 1998). A branch-and-bound search of the data returned a single most parsimonious cladogram, which is shown in Figure 3. The relationships shown in the cladogram are compatible with those reported by Tehrani and Collard (2009b) in a previous analysis of these data, in which a different outgroup was used (Arab Bedouin). The fit between the cladogram and the data was measured using the Retention Index (RI) and bootstrapping. The Retention Index is a measure of the number of homoplastic changes that a cladogram requires independent of its length (Farris, 1989a, 1989b). A maximum RI of 1 indicates that the cladogram fits perfectly with the dataset, whereas the worse it fits, the closer the RI score approaches 0. The RI of this cladogram was 0.62. Simulation work (see Nunn et al., this issue) suggests that a RI as high as this provides strong evidence that these assemblages evolved by descent with modification from ancestral assemblages. The phylogenetic bootstrap is a technique for measuring support for individual clades (Felsenstein 1985). It involves generating cladograms by creating “pseudo” data sets the same size as the original by randomly re-sampling characters from the original data set with replacement a large number times (in this case, ten thousand) and calculating the percentage of replicates that support a given

clade. As can be seen in Figure 3, all of the relationships were supported by a large percentage of the bootstrap replicates.

FIGURE 3 ABOUT HERE

Several of the relationships indicated in the cladogram are consistent with ethnohistorical and linguistic evidence about the relationships among the populations, while several others are not. The finding that the weavings of the Yomut and Tekke are descended from an exclusive common ancestor is compatible with the fact that both populations speak the same Turkic language, Turkmani. Similarly, the finding that the assemblages of the Bakhtiari and Boyer Ahmad are more closely related to each other than they are to those of any other group is supported by the fact that they both speak closely related dialects of Lori and inhabit the same area. However, contrary to ethnohistorical and linguistic evidence, the assemblages of the two Lor groups appear to be more closely related to those of Turkic speaking groups (the Yomut, Tekke, Qashqa'i and Shahsevan) than they are to the other Indo-Iranian-speaking group, the Baluch. Furthermore, the cladogram suggested that the Qashqai and Shahsevan share a more recent common ancestor with the three Lor-speaking groups than they do with the Yomut and Tekke, which again contradicts linguistic groupings. Lastly, the Qashqai assemblage appears to be more closely related to those of the Boyer Ahmad and Bakhtiari than it is to the Shahsevan, even though the latter speak a closely related dialect of the same language.

To assess the importance of these differences, we compared the number of changes required by each character on the most parsimonious tree to the number of changes required by a tree in which the relationships among the assemblages were forced to reflect the tribes' population histories. The difference in the character lengths was then evaluated using a one-tailed Wilcoxon sign-ranks test, as described by Templeton (1983). The analysis found that the population tree required a significant number of extra steps compared to the most parsimonious tree (total number of extra steps = 38, $p > 0.01$). Thus, the strong phylogenetic signature recovered from the textile data cannot simply be accounted for purely in terms of descent with modification from common ancestral populations.

To shed more light on the relationships between the population history of the tribes and their weaving traditions, we carried out a cophylogenetic analysis in which the best estimate of tribal population history was treated as the independent phylogeny and the cladogram derived from the weaving data was treated as the dependent phylogeny. Previous efforts to apply cophylogenetic techniques to cultural evolution (e.g. Jordan and Mace 2006, Riede 2009) were limited by methods that only mapped three types of relationships between the independent and dependent phylogenies: codivergences, sorting events and duplications. They were therefore unable to address the potential role played by horizontal transfers in generating mismatches between the compared trees. Here, we were able to overcome this constraint by using the program TreeMap 2.0 (Page & Charleston 2002), which implements an algorithm called ‘jungles’ (Charleston 1998). Jungles is an advancement on previous tree reconciliation methods because it considers all four cophylogenetic processes, including horizontal transfer.

First, a jungles analysis generated all the possible solutions to the cophylogeny of the craft tree and population tree. The total cost of each solution was then estimated according to the number of events other than co-divergences that they hypothesised. Solutions with lower costs are considered preferable to those with higher costs, since the latter require a greater number of independent evolutionary events to explain how the observed patterns of association between the two sets of entities arose. This approach is known as “event-based parsimony” (Ronquist 1996). In principle, it is possible to impose additional optimality criteria by assigning different costs to each type of event. However, for the purposes of this study we assumed that there is an equal likelihood of horizontal transfers, duplications and sorting events and therefore assigned the same cost (1) to each of them (with a cost of 0 for co-divergences).

Figure 4 shows three different solutions to the cophylogeny of the craft tree and language tree returned by TreeMap. Figure 4a hypothesises four co-divergences and two horizontal transfers. Thus, the total cost of the reconciliation between the two trees is 2. Figure 4b also has a reconciliation cost of 2. It hypothesises five co-divergences and one horizontal transfer and a sorting event. Figure 4c hypothesises a reconstruction of events that involves no horizontal transfers. Instead, it suggests that there were three duplications early in the history of weaving that gave rise to several

distinct craft lineages. All the lineages subsequently underwent extensive pruning as a result of sorting events that occurred at each juncture where ancestral populations split into new ones. In total, the jungle proposes three duplications and eight sorting events, with a total reconciliation cost of 12.

FIGURES 4 ABOUT HERE

To test the validity of these various explanations, a further analysis was carried out that involved randomising the associate tree and measuring how often the randomised trees fit as well as the original tree. The results of this analysis suggested that the number of events hypothesised by both the first two jungles was significantly fewer ($p < 0.05$) than the number of events that would be required to explain associations between the population tree and random trees. In contrast, the number of events hypothesised by the third jungle was not less than what would be expected by chance. We can therefore reject the hypothesis shown in Figure 4c.

The analyses were unable to distinguish which of the other two reconstructions represent a better explanation for associations among the tribes' weaving traditions and population histories. Both explanations were found to be statistically significant and both had the same cost (2). Since we currently lack convincing reasons to assume that horizontal transfers are either more or less costly than sorting events, we cannot reject *a-priori* an explanation that requires two horizontal transfers (Figure 4a) in favour of one that requires only one horizontal transfer but also one sorting event (Figure 4b) or vice versa. We can however judge the merits of each reconstruction against other existing lines of evidence.

The horizontal transfers hypothesized in Figure 4a are compatible with geographical evidence and historical records. The hypothesis that the ancestor of the Bakhtiari and Boyer Ahmad acquired weaving from the ancestor of the neighbouring Qashqai is consistent with the fact that they are close neighbours. It is also compatible with ethnohistorical data suggesting that the ancestors of the Qashqai arrived in the region prior to the divergence of the Bakhtiari and Boyer Ahmad. As noted earlier, whereas the ancestors of the Qashqai are believed to have migrated to their present day territories in southwestern Iran some 500 years ago (Oberling 1974), the Bakhtiari and

Boyer Ahmad did not emerge as distinct tribal entities until the 18th/19th century (Amanolahi 1988, Garthwaite 1983). It is therefore plausible that the Bakhtiari and Boyer Ahmad inherited weaving from a common ancestor that had adopted it as a result of contact with the ancestors of the Qashqai.

The other horizontal transfer hypothesized in Figure 4a occurs between the ancestor of the Shahsevan, Qashqai, Tekke and Yomut and the ancestor of the Baluch. As mentioned previously, the Baluch are thought to be descended from a tribe that migrated from the southern Caspian Sea to southwestern Iran some 900 years ago. This event is roughly contemporaneous with (and may perhaps have even been caused by) the expansion of Oguz Turks into western Iran in the 11th and 12th centuries (Thomson 2002), from who the Shahsevan and Qashqai are descended (Oberling 1974). It is certainly possible, therefore, that the Baluch split from the Boyer Ahmad and Bakhtiari before the Shahsevan and Qashqai split from the Tekke and Yomut, and that all five groups acquired their weaving traditions from a common Oguz Turkic source.

The explanation in Figure 4b also hypothesizes a horizontal transfer from the ancestor of the Qashqai to the ancestor of the Bakhtiari and Boyer Ahmad. As pointed out above, this scenario is plausible in the light of the historical evidence. However, instead of assuming that the Baluch acquired weaving from the ancestor of the Tekke, Yomut, Qashqai and Shahsevan, Figure 4b suggests that the weavings of the Baluch are derived from an ancestral Iranian tradition that went extinct in the Boyer Ahmad-Bakhtiari lineage. It further indicates that the relationship between the weavings of the Baluch and those of the Shahsevan, Qashqai, Tekke and Yomut can be explained by descent from a common ancestor of both Turkic and Iranian-speaking groups. However, given that the best estimate from historical linguistics (e.g. Gray & Atkinson 2003) is that the relationship between Turkic and Iranian languages probably predates the origins of agriculture and therefore the keeping of animals for wool, this hypothesis seems unrealistic. It is more plausible that Baluchi weaving traditions, like those of the Boyer Ahmad and Bakhtiari, were originally borrowed from Turkic peoples their ancestors came into contact with. On that basis, we believe that the reconstruction of events as shown in Figure 4a represents the best explanation for the origins and spread of weaving among the populations.

Discussion and conclusions

Phylogenetic approaches to cultural diversity have shown that the diversification and spread of cultural traditions is often closely linked to the dispersal histories of populations (e.g. Mace et al. 2005, Lipo et al. 2006, Collard et al. 2006). The findings of our case study lend further weight to this evidence. Borrowing techniques from biology that are designed to study coevolutionary relationships, we found that relationships between Iranian tribal craft traditions and population histories could be largely accounted for in terms of “co-divergence” – the parallel cladogenesis of one lineage with another. Thus, in the two best reconstructions returned by the analyses, all of the relationships among the Turkic tribal assemblages could be explained by population phylogenesis, as could the relationship between the assemblages of two of the Iranian-speaking groups, the Boyer Ahmad and Bakhtiari.

Nevertheless, it was also clear that some of the relationships between textile assemblages were incompatible with data on the groups’ population histories. Following other researchers (e.g. Jordan & Mace 2006), we have suggested that such anomalies can be explained in relation to dual inheritance theory whereby, just as individuals can copy cultural behaviours from role models other than their parents, populations may sometimes acquire traditions from sources other than their immediate ancestors. However, as biologists have long known, horizontal transfers are not the only cause of discrepancies between co-evolving systems. In order to estimate horizontal transfers accurately, it is crucial to consider the possible roles played by sorting events and duplications, both of which have direct analogues in cultural evolution.

Using the jungles algorithm, we were able to evaluate the likely role played by each of these processes in generating the conflicts between the textile phylogeny and population tree. Two of the reconstructions returned by the analysis involved horizontal transfers, while a third did not. Since the latter required a significantly greater number of events than the other two, it was rejected. The two remaining reconstructions were equally parsimonious. One required two horizontal transfers, while the other required one horizontal transfer and one sorting event. By comparing

both reconstructions to other sources of evidence, we concluded that the former was the more realistic scenario. Thus, having considered and ruled out the alternatives, we can be reasonably confident that in this case horizontal transfers are likely to be the major source of inconsistencies between the textile phylogeny and the population phylogeny reconstructed from linguistic data and oral histories.

Of course, like weaving, both language and oral histories are socially transmitted, and as such cannot be regarded as unproblematic guides to population history. Some studies suggest that mismatches between language and genetic history are common among pastoralist populations in the Middle East (Nettle & Harriss 2003), and that oral accounts of group origins can be ambiguous or misleading. As Barth (1961) explained in his classic study of nomads of South Persia, linguistic and ethnic identities are often based on a group's political affiliations, rather than its actual historical origins. Barth (1961) describes several cases where groups are known to have adopted the language of politically dominant groups, initially becoming bilingual but ultimately switching completely to their new tongue. Thus, in the absence of genetic data, we cannot be certain that language and oral history provide an accurate reflection of group histories. Instead they and the weaving traditions may represent different "packages" of cultural inheritance (e.g. Boyd et al. 1997), whose descent histories differ from each other and from the "true" population history of the tribes.

An even more intriguing possibility is that these traditions are all tracking population histories, but *different* aspects of population history. Thus, whereas weaving is transmitted down the female line, oral history and ethno-linguistic affiliations are usually traced via males. Studies of population genetics in other patrilineal pastoralist groups in the region suggest that there are often differences in the migration histories of males and females in these populations, which can occur as a result of some patrilineal groups expanding into others' territories and then marrying with local females (e.g. Chaix et al., 2007, Perez Lezaun, 1999). The complexities of human genetic and cultural histories here and elsewhere mean that in most cases there will not be a single phylogeny for either populations or their traditions. Reconciling these diverse lineages of inheritance is likely to present us with significant challenges. Fortunately, the

progress that has been made in addressing similar problems in biology means that we are well equipped to face them.

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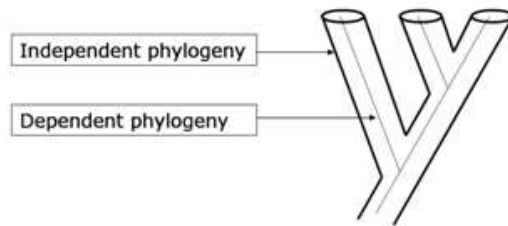
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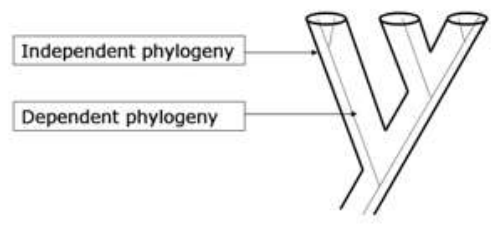
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Figures:

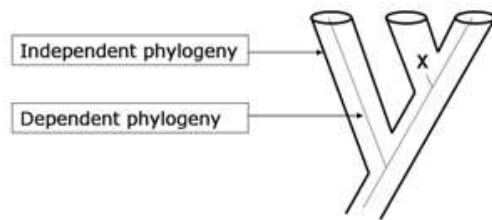
a) co-divergence



c) duplication



b) sorting event



d) horizontal transfer

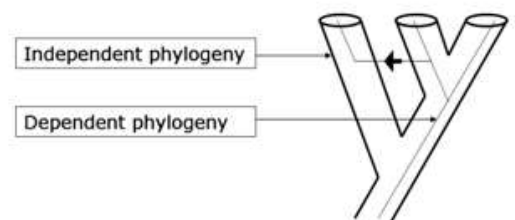


Figure 1. Terminology of historical associations between a dependent (parasite) phylogeny and independent (host) phylogeny.

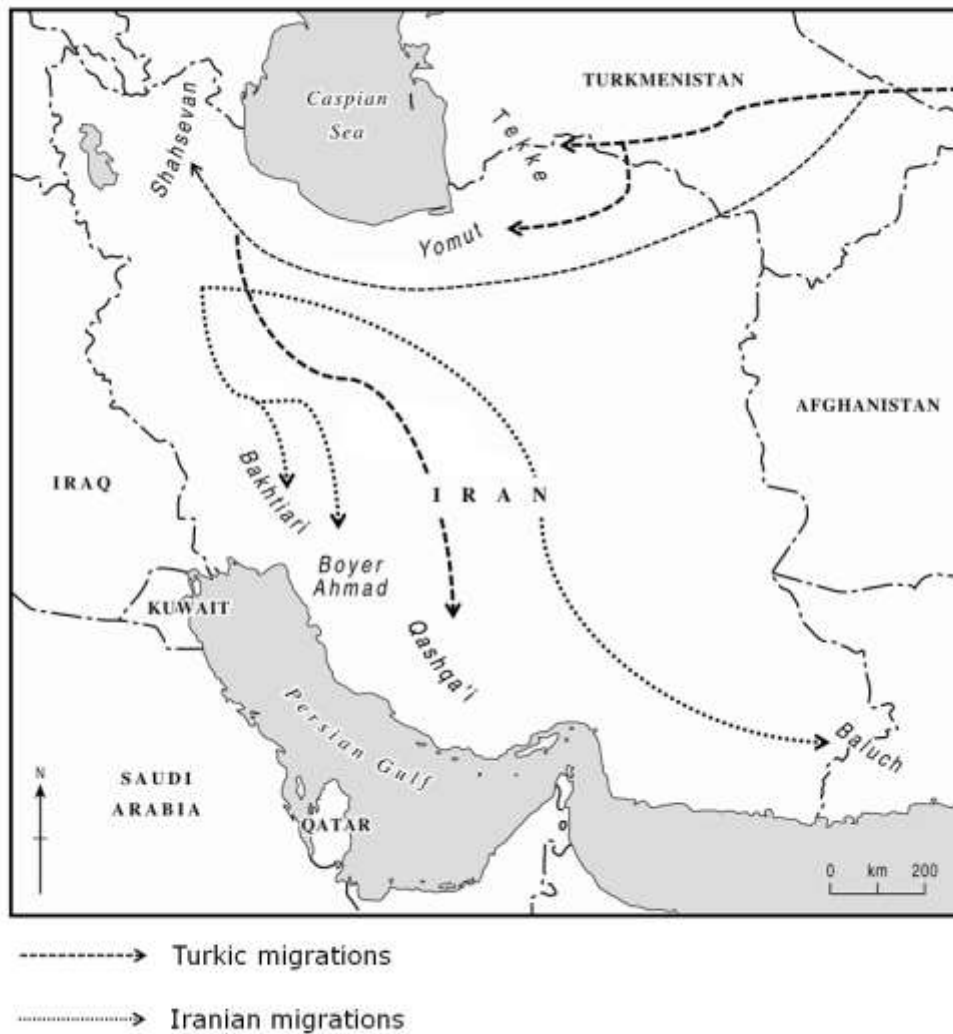


Figure 2. Map showing locations of Iranian tribal populations included in the case study and their approximate migration histories.

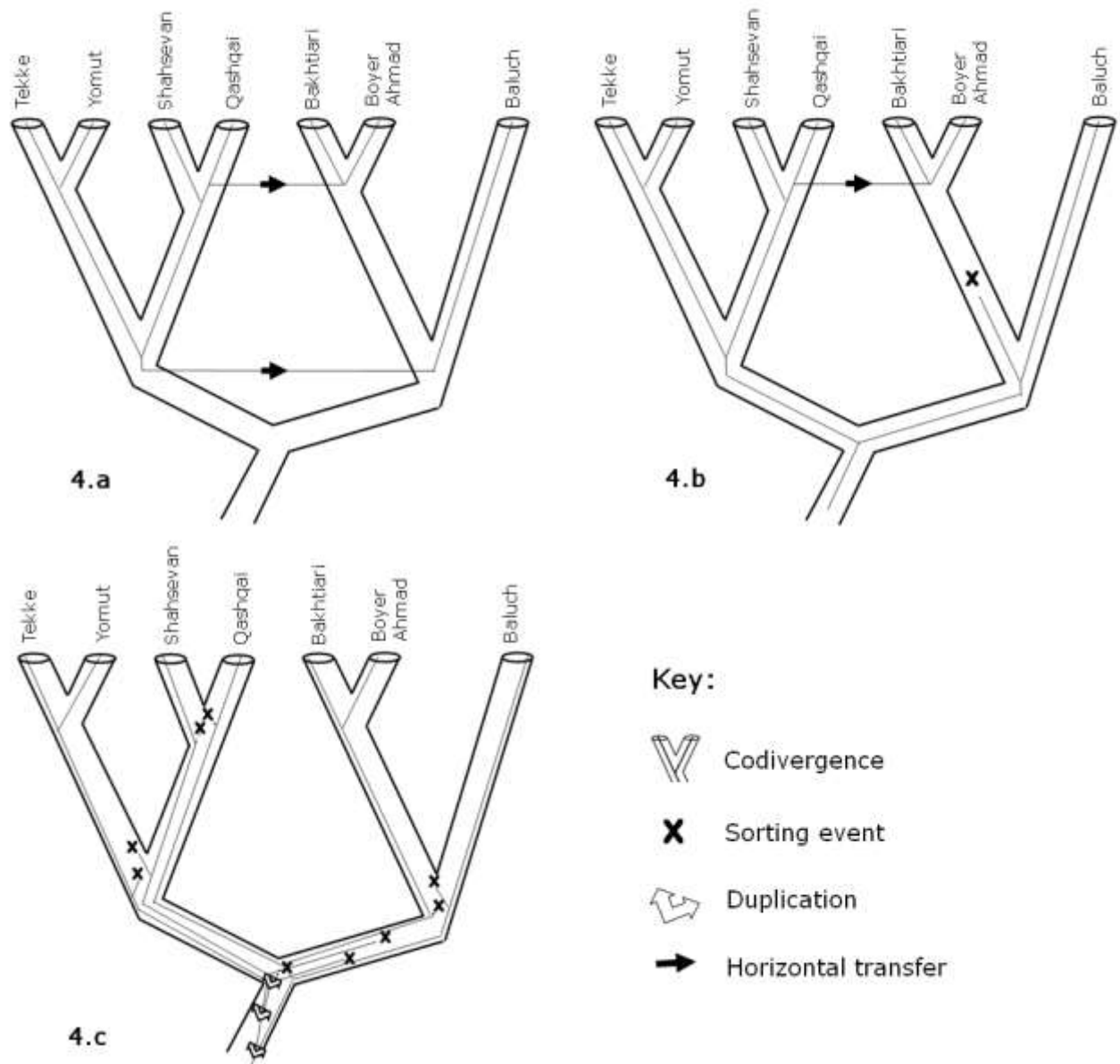


Figure 4. Three solutions to the cophylogeny of the tribes' weaving traditions and population histories, as reconstructed in TreeMap 2.0. The independent tree (hollow cladogram) represents the populations' histories, while the dependent tree (solid lines) represents the history of their craft traditions. The different events hypothesised in each reconstruction are indicated by symbols that are explained in the key.